

# A COMPARATIVE STUDY OF THE INFLORESCENCE IN FOUR SPECIES OF *SCHOENOXIPHIMUM* AND ITS SIGNIFICANCE IN RELATION TO *CAREX* AND ITS ALLIES.

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The genus *Schoenoxiphium* was established by Nees von Esenbeck in 1832 (*Linnaea* VII, p. 531). The type species he named *Schoenoxiphium capense*, but as this species had already been called *Schoenus lanceus* by Thunberg (*Prod. Pl. Cap.*, p. 17, 1794) the older epithet *lanceus* must be retained. The combination *Schoenoxiphium lanceum* was made by Kükenthal in 1909 (*Das Pflanzenreich* IV, 20, p. 28). This species is common in shady ravines on Table Mountain and is one of the species to be discussed.

In 1836 Nees (*Linnaea* X, p. 200) added three further species to *Schoenoxiphium*, two of which *S. Ecklonii* and *S. Thunbergii* occur on the Cape Peninsula on open bushy slopes. Since then these species have suffered various vicissitudes both as regards names and status, so it is desirable at this point to give reasons for adopting Nees' original names. *S. Thunbergii* is very common on the slopes around Lion's Head and is the only species occurring there. It also occurs on Devil's Peak. These localities are cited by Nees, so although his description is not full enough for complete certainty, the localities indicate clearly the particular species to which he referred. Clarke in 1883 retained this plant as *S. Thunbergii* (*On Hemicarex and its allies. Journ. Linn. Soc.* XX, p. 374), but later in *Flora Capensis* VII (1898) he changed his mind and placed it in *Carex*. As the name *Carex Thunbergii* was occupied he named it *Carex bisexualis*. In 1909 Kükenthal returned it to *Schoenoxiphium* as a variety of *S. Ecklonii* under the name *S. Ecklonii* var. *unisexualis*. The result of the present investigation makes it clear that the plant differs from *S. Ecklonii* in so many features that its claim to specific rank cannot be disputed and it thus reverts to the original name given to it by Nees.

*S. Ecklonii* is a widespread species in the Cape Province. The localities cited for it by Nees are all in the eastern part of the Province and it is probable that the early plant collectors did not find it on the Cape Peninsula where it occurs in more inaccessible places than the super-

ficially similar *S. Thunbergii*. It is a common plant on the slopes of Karbonkelberg near Hout Bay and occurs rather infrequently in scattered localities over the whole peninsula.

The fourth species with which this paper is concerned is *S. Lehmannii* (Nees) Steud., a slender plant growing in similar situations to *S. lanceum* but much less common. It was originally described by Nees as a species of *Uncinia*. Kunth (Enum. Pl. II, p. 528, 1837) retained it in *Uncinia* but remarked that it seemed to be more like *Schoenoxiphium* to which genus Steudel (Syn. Pl. Glum. II, p. 245, 1855) eventually assigned it. Clarke (Flora Capensis VII, p. 304) named it *Carex esenbeckiana* Boeck. while Kükenthal a few years later reduced it to varietal rank under the name *Schoenoxiphium sparteum* var. *Lehmannii*. A complete revision of *Schoenoxiphium* may show that this plant is too close to *S. sparteum* to merit separate specific rank. The writer's experience has led her to endorse Clark e's remarks on the difficulties which this genus presents to workers on dried herbarium material. Delicate structures which are clearly discernible in fresh material are easily overlooked in dried specimens. Until a revision based on fresh material can be undertaken it seems best to treat the plant as a distinct species, a procedure which is adopted here.

All workers on the Caricoideae have found difficulty in placing the boundaries of the genera. That this is true of *Schoenoxiphium* will be obvious even from the histories given in the previous paragraphs of the four species under discussion. Nees, the founder of the genus, separated it from *Carex* on the presence of an axis within the sheathing bract (utricule) of the female flower, whereas according to his definition *Carex* lacked this enclosed axis. Later when it became obvious that some species generally accepted as belonging to *Carex*, had a small axis within the utricule, Nees' original definition was clearly inadequate and other distinguishing features were sought. Later authors tended to make use of the utricule. Thus Clarke in the Flora Capensis retained in *Schoenoxiphium* only those species in which the utricule is deeply split down one side and placed the rest in *Carex*. Kükenthal, too, in his monograph of the Caricoideae stressed the incompletely closed utricule of *Schoenoxiphium* as opposed to the closed utricule of *Carex*. However, his conception of the genus was somewhat different from that of Clarke and he returned to *Schoenoxiphium* many of the species transferred to *Carex* by Clarke. As a result of the present investigation it will be seen that the utricule which was stressed by both these authors is an extremely variable structure even in a single inflorescence. It must therefore be used as a diagnostic character with extreme caution. "The wheel is come full circle" and we find ourselves back at the point from which Nees started,

with the most significant difference between the two genera being the flattened axis within the utricle in the case of *Schoenoxiphium*.

Many facts not recorded in previous accounts of these species have been discovered as a result of intensive studies of fresh material. The object of this paper is therefore to give a comparative account of the inflorescences of these four species. Light is thrown on evolution in the Caricoideae and the results are in consequence of more than local interest.

The inflorescence is racemose, consisting of a main axis bearing leafy bracts which may or may not have a closed sheath. In the axils of these leafy bracts secondary axes occur which may be elongated as in *S. lanceum* or compact as in *S. Ecklonii* and *S. Thunbergii*. In *S. Lehmannii* the lateral branches are somewhat lax and few-flowered. If the lowest secondary axis occur low on the main axis it may be somewhat reduced, but with this exception it is generally true that the lower secondary axes are the best developed and a gradual reduction in complexity occurs towards the apex of the main axis. All the secondary axes analysed in this paper were vigorous and taken from the lower half of the whole inflorescence.

### **S. Ecklonii.**

The sheath of the leafy bracts on the main axis may be closed for a considerable distance at the base of the inflorescence in well developed specimens but the sheath is gradually reduced until in the uppermost bracts no sheath at all is found. Fig. 1 A is a diagrammatic representation of a well developed secondary axis, with all the internodes considerably elongated. At the base is a sheathing bract. If the secondary axis happen to arise in the axil of a leafy bract with a well developed sheath, this sheathing bract is exceedingly delicate in texture, closed almost to the top and completely hidden. In such cases it is easily overlooked and in dried material is almost impossible to see. In the upper part of the whole inflorescence the leafy bract has a reduced sheath or none, and in such cases the sheathing bract at the base of the secondary axis is firm and only closed in its lower half (Fig. 2 A, B.) While in the lower part of the whole inflorescence the sheathing bract at the base of each secondary axis is sterile, in the upper part it encloses a female flower as well as the axis. The secondary axis grows through the sheathing bract and bears along its length bracts of the type shown in Fig. 2 C. The structures arising in the axils of these bracts are inflorescences (either compound or simple) in the lower part, and male flowers towards the apex. These are shown diagrammatically in Fig. 1 A. It will be noted



FIG. 1.

[See opposite.]



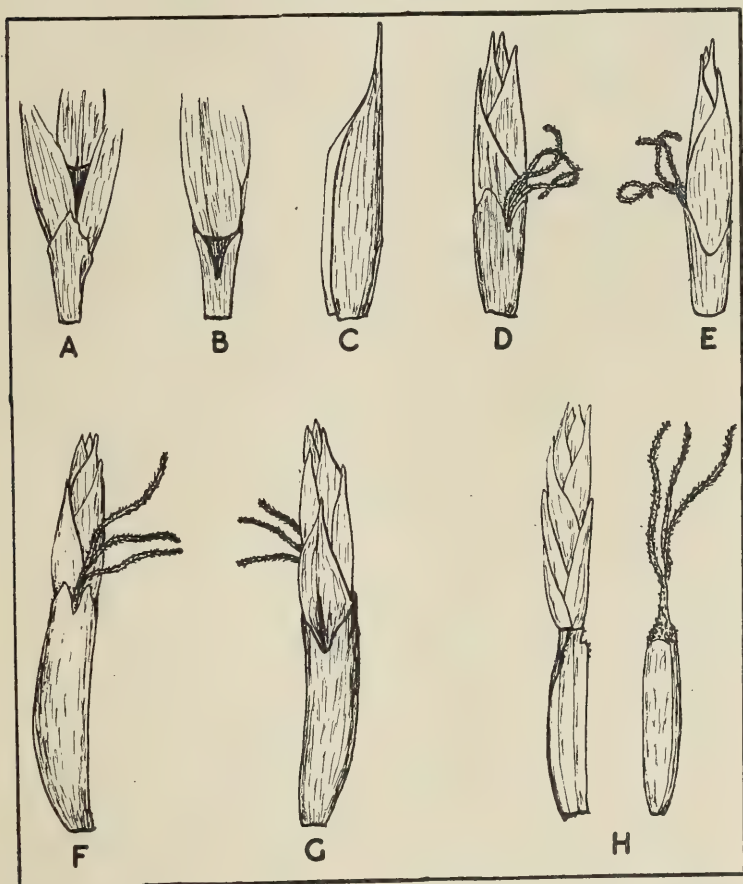


FIG. 2. *S. Ecklonii*: A. Back view of a sterile utricle at the base of a secondary axis; B. Front view of the same; C. One of the bracts arising on the secondary axis; D. Back view of one of the first fertile utricles to be borne on a secondary axis; E. Front view of the same; F. Back view of an upper fertile utricle on a secondary axis; G. Front view of the same; H. Female flower and flattened axis bearing male flowers from within the utricle shown in F and G. All  $\times 3$ .

FIG. 1. A. Diagram showing the structure of a secondary axis in *S. Ecklonii*. In this and in Figs. B, C, D, E, symbols are used to denote male and female flowers. Utricles are shaded and all internodes are elongated.

B. Diagram of a secondary axis in *S. lanceum*.

C. Diagram of a secondary axis in *S. Thunbergii*.

D. Diagram of a secondary axis in *S. Lehmannii*.

E. Diagram of the base of a vigorous secondary axis in *Carex clavata*.

that at the base of each of the tertiary axes a sheathing bract occurs similar to that at the base of the secondary axis. In the two lowest tertiary axes the sheathing bract contains nothing but an axis, but in the third from the base and all subsequent to that a female flower occurs within the sheathing bract on the side nearest the secondary axis. Bracts are borne on the tertiary axes similar to those borne on the secondary but becoming progressively smaller. On the two lowest tertiary axes the first ordinary bract bears in its axil a sheathing bract within which is a single female flower and a reduced axis bearing sterile bracts at the apex. Apart from these two axes the others bear male flowers only in the axils of their bracts. From the diagram it is clear that in this species the female flower is always borne within a sheathing bract, accompanied by an axis which normally bears one to several male flowers at its tip. The only exception to this is the one noted above. However, in a particularly vigorous specimen examined, male flowers were developed on the quaternary axes as well. In less vigorous inflorescences the first tertiary axis may proceed directly from the basal empty sheathing bract to bracts bearing male flowers. In other cases the two tertiary axes of the type shown at the base of the secondary axis may be omitted.

The sheathing bract which invariably occurs at the base of each lateral axis, whatever its position, shows a considerable range of form. Fig. 2 A, B show back and front views of a sterile sheathing bract at the base of a secondary axis. One of the lowest fertile sheathing bracts, such as that at the third node in Fig. 1 A, is depicted in Fig. 2 D, E. Fig. 2 F, G give corresponding views of the most common type of sheathing bract, found in the upper part of the inflorescence. Fig. 2 H shows the female flower and male axis within this type of bract. It will be seen that whereas the basal sheathing bracts are split more than half-way down at the front, the bracts higher up the inflorescence are open in front for a short distance only. It is obvious that such a variable feature as this cannot be made a matter of primary importance in distinguishing genera. From a comparative study of the inflorescence as a whole it becomes clear that the sheathing bract, whether it contains a female flower or not, is the morphological equivalent of a utricle. Consequently in future descriptions given here the term utricle will be used in this extended sense for sheathing bracts of this type.

### ***S. lanceum.***

This species is much larger than the others with which this paper deals. Although superficially the inflorescence looks very unlike that of *S. Ecklonii* owing to its elongated internodes, in reality it is built up on a very similar plan, though slightly more elaborate. As before, the

main axis bears a number of leafy bracts in the axils of which secondary axes arise. Each secondary axis is sheathed at the base by a utricule (Fig. 3 A) which in the lower part of the whole inflorescence is devoid of a female flower but which higher up contains a female flower as well as an axis (Fig. 3 B, C). Fig. 3 D shows the back view of a typical utricule in the middle part of any axis. The tertiary axes are better developed in this species though they show exactly the same type of progressive simplification as the apex of the secondary axis is approached. Fig. 1 B, which is a diagram of a secondary axis, will bring out the differences between this species and *S. Ecklonii*. Every utricule, excluding the basal, encloses a female flower though occasionally in the upper part this may be abortive. All the quaternary axes bear male flowers, whereas in *S. Ecklonii* this is exceptional. In general, however, the fundamental plan is the same.

### **S. Thunbergii.**

This species has only been recorded in the neighbourhood of Cape Town while both the previous species have a fairly wide range within the Cape Province. The chief significance of *S. Thunbergii* lies in the clear indications it gives of the evolutionary trends within the Caricoideae which ultimately culminated in *Carex*, the most highly specialised genus in this sub-family. The inflorescence is much like that of *S. Ecklonii*. Fig. 1 C shows a diagram constructed from a well developed secondary axis. The same general features that have been described fully for *S. Ecklonii* are present here but with one important difference. Of the tertiary axes only the lower ones bear male flowers. In the majority of cases the tertiary axis, which is not unlike that of *S. Ecklonii*, remains hidden within the utricule and merely bears one or two reduced bracts at the apex. Viewed from without, this type of utricule might well belong to a species of *Carex* as it is completely closed and has two lateral tooth-like processes at its tip (Fig. 3 H, J). With the removal of the utricule the conspicuous, flattened tertiary axis is easily seen (Fig. 3 K). All utricles are not of this type. Fig. 3, G shows the form it assumes when the axis extends through the utricule and bears male flowers. Fig. 3 E, F show the broad, wide-mouthed type which is found at the base of the secondary axis.

### **S. Lehmannii.**

This species is confined to sheltered places in ravines on the eastern side of Table Mountain. The lateral inflorescences occur in the axils of somewhat distant leafy bracts much as in *S. lanceum*, but in all other

respects the two species are dissimilar. *S. Lehmannii* is a much smaller plant, has relatively few flowers on each lateral axis and simple androgynous inflorescences are rare. Fig. 1 D is a diagram of a well developed secondary axis. A peculiarity of this species lies in the marked intervals of time that occur between the maturation of the flowers on successive axes of any one lateral inflorescence. Thus in an inflorescence such as that shown in the diagram if the flowers borne directly on the principal axis were fully developed, then those on the two basal lateral axes would be immature. On the single axis of a still lower degree the flowers would be so immature that their parts could only just be made out. Frequently when these youngest flowers reach maturity all that is left of the first formed flowers are scars on the axis. No attempt is made in the diagram to indicate the relative ages of the flowers on the different axes.

In the upper part of the whole inflorescence the lateral axes are rather less well developed than in the example illustrated in Fig. 1 D. In most cases only the basal lateral axis bears more than one flower and it may be much more reduced than those shown in the diagram. The basal utricle in such cases may contain a female flower and the axis enclosed by the utricle and growing beyond it, bear a few male flowers. Such simple androgynous inflorescences, however, are much less common in this species than in the first three. Most of the female flowers are borne within a closed utricle which narrows to a pronounced neck (Fig. 3 L). The axis arising within the utricle is exerted and bears one or two minute sterile bracts at the apex.

#### THE STATUS OF *SCHOENOXIPHIMUM THUNBERGII*.

A comparison of the diagrams and figures of *S. Ecklonii* and *S. Thunbergii* makes it quite clear that they are two distinct species. The inflorescence, the utricle and the ovary all provide easy means of separating them. In vegetative habit, too, they are different. *S. Ecklonii* has long stolons which extend for some distance from the parent plant so that new growths do not arise close to the old, whereas *S. Thunbergii* has very short lateral underground branches which result in a tufted habit.

#### DISCUSSION.

The nature of the utricle is clearly demonstrated in these species of *Schoenoxiphium*. On lateral axes of all degrees the lowest bract is always united by its edges to form a sheath through which the axis continues. The degree of union is variable not only in the different species but also on different parts of the same inflorescence. In the majority of cases a female flower arises in the axil of this bract or utricle, though towards the base of the secondary and tertiary axes a flower in



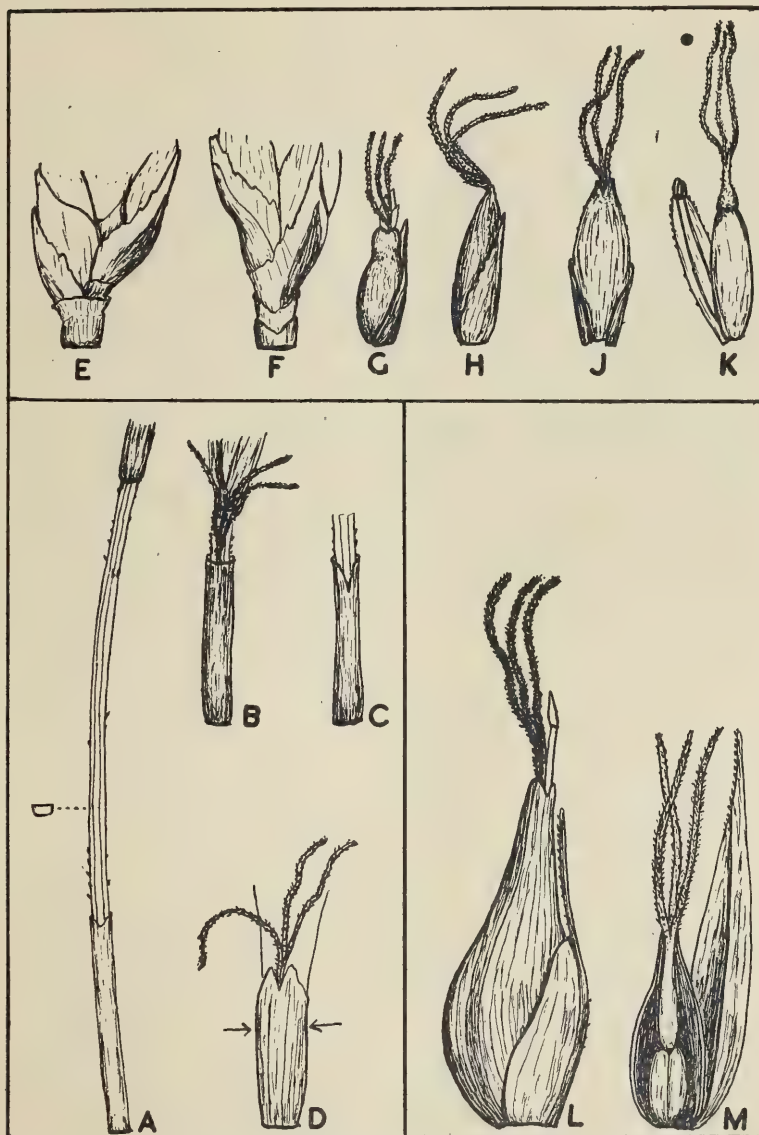


FIG. 3. A—D. *S. lanceum*: A. Sterile utricule sheathing the base of the secondary axis; B. Back view of the first fertile utricule; C. Front view of the same; D. Back view of a typical utricule. In the specimen drawn the opening down the front extended to the level of the arrows. The degree of opening is somewhat variable.

E—K. *S. Thunbergii*: E. Back view of a sterile utricule at the base of a secondary axis; F. Front view of the same; G. Utricule and its subtending bract from the third node in Fig. 1C; H. Utricule of an upper flower with its subtending bract, side view; J. The same, front view; K. Female flower and flattened axis with the utricule removed.

L. *Schoenoxiphium Lehmannii*. Female flower with utricule and subtending bract; the axis seen protruding through the mouth of the utricule.

M. *Carex aethiopica*. Female flower and subtending bract, half the utricule removed; showing the minute axis at the base of the ovary.

A—K.  $\times 3$ ; L, M.  $\times 10$ .

this position may be lacking. A comparison, however, of successive lateral branches from the same inflorescence makes it clear that it is largely a matter of position and vigour which determines whether a female flower will develop or not. In vigorous lateral axes near the base of the inflorescence some empty utricles are always found, whereas in less well developed axes near the base in stunted plants and in the upper axes of all specimens, every utricle contains a female flower. The male flowers, too, are quite consistent in their positions. They occur in the axils of normal bracts towards the apices of axes of any order. The minor axes show a strong tendency to lose the capacity for producing male flowers, a feature clearly seen in *S. Thunbergii* where the male flowers are largely confined to the apices of the primary and secondary axes.

This process is carried to its logical conclusion in *Carex* where the male flowers with few exceptions arise towards the apices of the primary and secondary axes. The upper inflorescences are wholly male, the lower either female in the lower part and male at the tip, or female throughout. The South African species of *Carex* examined have no obvious axis within the utricle, but species occur in the northern hemisphere in which a small but easily recognised axis is present. However, it is never a large flattened structure such as characterises *Schoenoxiphium*.

*Schoenoxiphium* is usually regarded as a primitive member of the sub-family Caricoideae and the observations recorded here strengthen that view. As a matter of interest three local species of *Carex* were examined in order to compare their inflorescences with those of *Schoenoxiphium*. These species were *C. aethiopica* Schkuhr, *C. clavata* Thunb. and *C. Ecklonii* Nees. All showed agreement in general features of the inflorescence. Each secondary axis is sheathed at its base by a sterile utricle. When the secondary axis is concealed for some distance by the sheathing base of the leafy subtending bract, the utricle is a delicate translucent sheath wholly devoid of colour. Towards the upper part of each whole inflorescence the sheath of the subtending bract becomes shorter and at the same time the utricle becomes firmer and gradually assumes a green tinge.

In vigorous specimens of *C. clavata* many of the lower female inflorescences are compound at the base. The sequence of structures in such cases is shown in Fig. 1 E which is a diagrammatic representation of the lower part of a female inflorescence of this type, constructed on similar lines to those given for *Schoenoxiphium*. In the axils of the four lowest bracts utricles are seen enclosing a female flower. An axis bearing fertile bracts continues through it. A comparison of this diagram and

that given for *S. lanceum* (Fig. 1 B) shows that the two inflorescences are based on the same general plan. The chief difference lies in the much greater length to which reduction of the lateral axes has been carried in *Carex*. The fifth and sixth bracts in the diagram subtend a female flower and a reduced axis surrounded by a utricle. Fig. 3 M illustrates such an axis in *C. aethiopica*. Every utricle above this level contains a female flower only, the type of structure regarded as typical of *Carex*. As in *Schoenoxiphium* the shape of the utricle varies with its position and according to the structures enclosed by it. The sterile basal utricles are delicate in texture and cylindrical in form. Those bearing a female flower and a fertile axis are firm and broad with a wide opening through which the axis passes. All subsequent utricles are much narrowed at the apex leaving only a small opening through which the style passes. These observations show that *Carex* and *Schoenoxiphium* agree closely in their fundamental plan. The evolutionary trends clearly discernible in *Schoenoxiphium* are carried to extreme lengths in *Carex* which taken by itself has many features not easily interpreted. It is interesting to note that as long ago as 1873 Bentham suggested that light might be shed on the morphology of the utricle by a more detailed knowledge of *Schoenoxiphium*. The knowledge now available justifies Bentham's belief.

The new facts recorded in this paper lead one to question the use of the term spikelet for members of the subfamily Caricoideae. The spikelet is generally accepted as the unit of inflorescence in Gramineae and Cyperaceae. While this is true of Gramineae it has been proved that the so-called spikelets of Cyperaceae are not all of the same nature. In Scirpoideae true spikelets are found, comparable with those of Gramineae. In Rhynchosporoideae the small inflorescences are cymose and therefore are not true spikelets. However, externally they cannot be distinguished from genuine spikelets and as a matter of practical convenience they will probably continue to be called spikelets. In Caricoideae, however, while the inflorescence is racemose throughout there is no simple unit such as a spikelet. *Schoenoxiphium* provides a key to the understanding of the inflorescence of this subfamily. Species such as *S. lanceum* and *S. Ecklonii* demonstrate clearly that each secondary axis, though highly complicated, is a complete unit in itself and cannot be resolved into still smaller units which would serve a useful purpose. As *Carex* is derived from an inflorescence of this type by reduction, the use of the term spikelet in the subfamily is undesirable.

#### ACKNOWLEDGMENT.

My thanks are due to Dr. L. Bolus for permission to use the library and collections housed in the Bolus Herbarium.